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Vision Research 48 (2008) 55–62

Vision Research

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Effects of perceptual learning on primary visual cortex activity in humans

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Received 27 August 2007; received in revised form 16 October 2007

Abstract

Psychophysical and neuroimaging studies suggest that perceptual learning may affect activity in primary visual cortex (V1). Yet, it remains unclear whether such changes involve intrinsic V1 plasticity or feedback from later processing stages. Here we recorded high-density electro-encephalography in 24 volunteers, 24-h after training on a visual texture discrimination task in the upper or lower visual-field. Post-training improvement in upper visual-field was associated with changes in early visual responses, starting 40 ms post-stimulus, with reduced amplitude of retinotopic C1, known to reflect V1 activity. No behavioral or neurophysiological effect was found after training in lower visual-field, suggesting retinotopic constraints on perceptual learning. Our results demonstrate that successful acquisition of a perceptual skill can produce long-lasting changes for initial sensory inputs in the adult human visual system.

Keywords: Perceptual learning; C1; EEG; Visual field asymmetry; Visual texture discrimination

1. Introduction

Through perceptual experience, the human brain learns to recognize the visual world and to distinguish fine sensory features that would remain undetected without practice. The specificity of improvement in some tasks (Karni & Sagi, 1991) suggests an involvement of the primary visual cortex (V1), as recently confirmed by functional magnetic resonance imaging (fMRI) studies in humans (Furmanski, Schluppeck, & Engel, 2004; Schwartz, Maquet, & Frith, 2002). However, it is still debated whether these post-training changes in fMRI responses in V1 arise primarily from local plasticity, or instead reflect feedback mechanisms exerted on V1 by top-down influences from later visual processing stages (Hupe et al., 1998; Mehta, Ulbert, & Schroeder, 2000) or fronto-parietal attentional networks (Schwartz et al., 2004).

To address this issue, we examined the precise time-course of perceptual learning using high-density electro-encephalography (EEG)[1] in human volunteers who were intensively trained on a classic visual texture discrimination task (TDT). Previous work has shown that training on such tasks may lead to long-lasting improvement in performance that is specific to the trained retinal location (Karni & Sagi, 1991; Stickgold, James, & Hobson, 2000) and associated with corresponding changes of fMRI responses within retinotopic V1 (Schwartz et al., 2002; Walker, Stickgold, Jolesz, & Yoo, 2005). Based on the hypothesis that TDT learning might involve local plasticity at the earliest

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[1] *Abbreviations used:* EEG, electro-encephalography; EOG, electro-oculogram; fMRI, functional magnetic resonance imaging; GFP, global field power; SOA, stimulus-to-mask onset asynchrony; TDT, texture discrimination task; V1, primary visual cortex; VEP, visual evoked potential, VF, visual field.

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doi:10.1016/j.visres.2007.10.027

cortical stages of visual processing, we predicted that visual stimuli presented at a trained location (relative to similar stimuli at an untrained location) should modify the initial cortical response imputable to V1 activity, as recorded by EEG (Clark, Fan, & Hillyard, 1995; Foxe & Simpson, 2002). Unlike EEG recordings, previous fMRI studies (Furmanski et al., 2004; Schwartz et al., 2002) did not have sufficient temporal resolution to establish the exact latency of V1 effects observed after TDT learning.

An extensive body of work has established that exogenous visual stimuli produce a characteristic sequence of electric potentials recorded by scalp EEG. Here, we tested for the effects of perceptual learning on the first of these visual evoked-potentials (VEP), the so-called C1 component (Jeffreys & Axford, 1972). C1 represents an evoked response in V1 (Clark et al., 1995) whose earliest portion reflects the initial volley of sensory afference in the visual system (Foxe & Simpson, 2002), prior to subsequent feedback from later stages of neural processing (Di Russo, Martinez, & Hillyard, 2003; Martinez et al., 1999; Noesselt et al., 2002). C1 polarity is typically reversed when stimuli are presented in the upper versus lower visual field, consistent with the cruciform organization of V1 around the calcarine fissure.

We exploited this electrophysiological property in our study by training two groups of participants with visual textures presented in either the upper or lower visual field. Post-training EEG was recorded 24 h later. During recording sessions, our participants performed TDT on targets presented at either the trained location or an untrained location in the opposite quadrant (Fig. 1A and B). All visual targets and their locations were thus physically similar but differed in terms of the previous training experience. Our results show for the first time that TDT learning can modify the earliest sensory response evoked within visual cortex for stimuli presented at the trained location, and that such effects may arise in the upper but not the lower visual field, indicating retinotopically specific constraints on TDT learning.

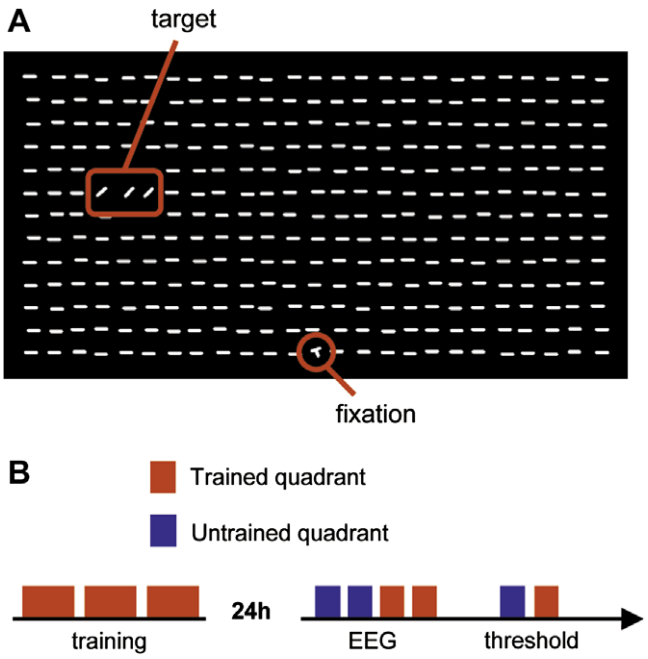

Fig. 1. Experimental paradigm. (A) TDT targets were three adjacent diagonal lines (vertically or horizontally aligned) presented in upper (or in lower) visual field. Participants had to discriminate target orientation, while fixating and reporting a central letter at the bottom (or top) of the display. (B) During training, targets always appeared within the same quadrant. During EEG recording (24 h later), targets appeared in the trained or, symmetrically, in the untrained quadrant across successive blocks. Performance threshold was then assessed for each quadrant separately.

2. Methods

2.1. Participants

Twenty-four volunteers (12 male; 25.2 ± 3.5 years) without neurological or psychiatric history gave informed consent to participate in our study, which was conducted in accordance with the Declaration of Helsinki and approved by the local Ethics Committee. All subjects had normal vision. Half of the subjects were trained and tested in the upper visual field (upper VF group), the others in the lower visual field (lower VF group), with equal numbers of males and females in each group.

2.2. Stimuli and behavioral task

We used the same task and stimulus parameters as described in previous work (Karni & Sagi, 1991). Texture displays were made of 13×25 high-contrast horizontal line-elements, presented either in the upper or lower visual fields (Fig. 1A). Targets consisted of three adjacent diagonal lines presented at varying positions (13–19° from fixation) and forming either a horizontal or a vertical array. A randomly rotated 'L' or 'T' also appeared at the bottom (top) of the display for the upper (lower) VF group, in order to impose fixation. The whole display covered 21×41 degrees of visual angle (1024×768 pixel screen resolution, 60 Hz refresh rate).

On each trial, a texture display was briefly flashed (16 ms), followed by a blank interval (stimulus-to-mask onset asynchrony, SOA), and then by a mask (100 ms) in which randomly rotated V-shaped elements replaced all line-segments (Karni & Sagi, 1991; Schwartz et al., 2002). New visual displays were generated on each trial, using a Matlab toolbox allowing precise presentation timing and synchronization with the EEG recording (www.vislab.ucl.ac.uk/Cogent2000). On each trial, participants first reported the central letter at fixation (T or L), and then judged the orientation of target-lines (horizontal or vertical), using four predefined keys (two for each task).

The training session was given 24 h prior to EEG recordings. During this session, participants performed TDT for three consecutive blocks (total 1260 trials, duration ~90 min; Fig. 1B), in which targets were always presented in the same quadrant (either right or left, counterbalanced across participants). The SOA between target display and mask was progressively reduced from 460 to 100 ms to establish learning (Karni & Sagi, 1991).

The EEG test session was recorded 24 h later, while participants performed the same task (4 blocks of 100 TDT trials each), but now with the targets shown in either the trained or the untrained quadrant (in AABB or BBAA order, counterbalanced across participants). During EEG recording, SOA duration was fixed at 500 ms so as to avoid any contamination of early VEPs by the mask presentation, and to rule out any spurious EEG effects due to mere differences in task difficulty or effort between the trained and untrained conditions.

Immediately following EEG recordings, a behavioral test phase was given to measure target discrimination thresholds for the trained and

untrained quadrants (80% correct responses), during which two series of 9 successive blocks (10 trials each) were presented in the trained and untrained hemifield with progressively decreasing SOAs (from 260 to 60 ms).

2.3. EEG recording and analyses

Scalp-EEG was recorded from 62 Ag/AgCl electrodes (Neuroscan, Synamps, El Paso, TX) positioned according to the extended international 10–20 EEG system; 30 K amplification, 0.01–100 Hz bandpass filter, and 50 Hz notch filter were used. Horizontal and vertical electro-oculograms (EOG) were monitored using 4 bipolar electrodes. EEG and EOG were acquired continuously at 500 Hz. Offline data processing included reduction of eye-blinks according to the procedure described by Gratton, Coles, and Donchin 1983; epoching from −50 to +450 ms around stimulus-onset; removal of epochs with EEG or residual EOG exceeding ±70 μV; and baseline correction over 50 ms pre-stimulus. Individual VEPs were then averaged and digitally low-pass filtered at 30 Hz.

Differences between conditions were first examined using the global field power (GFP) of EEG responses evoked by trained and untrained visual stimuli. GFP measures the strength of electric potentials concurrently recorded at all electrodes (rather than effects at a single electrode). We retained as significant any time-period during which GFP differed for 10 consecutive time-points (⩾20 ms) between trained and untrained conditions (paired *t*-tests, $p < .05$; cf. Guthrie & Buchwald, 1991).

We then identified the C1, P1, and N1 components based on their distinctive polarities, latencies, and topographic properties, and quantified their peak amplitude and latency in each participant. Because of the polarity inversion between upper and lower VF stimulation, we first computed learning-related changes by subtracting trained from untrained measures at each electrode for each subject before submitting them to standard ANOVAs (SPSS 15).

Finally, we tested for any topography differences between trained and untrained conditions during the C1 time-window (in addition to differences in amplitude or latency of this component), by using a microstate segmentation analysis (Pasqual-Marqui, Michel, & Lehmann, 1995). We also applied a Local Auto-Regressive Average (LAURA) procedure to estimate electric sources in the brain volume corresponding to the C1 scalp topography (Grave de Peralta Menendez, Murray, Michel, Martuzzi, & Gonzalez Andino, 2004). This distributed source localization method emulates the properties of neural generators by computing simultaneously active sources within the brain without any a-priori assumption on the number and position of generators.

3. Results

3.1. Behavioral data

During the training sessions, letter identification was high across the three successive blocks (>80%, >90%, >90%, respectively), for both the upper and lower VF groups, indicating that participants were able to maintain fixation equally well at all stages of training.

In contrast, texture detection thresholds (SOA at 80% correct) revealed a significant effect of training blocks [mean = 353 ms ± 131, 197 ms ± 49, and 184 ms ± 32 for blocks 1, 2 and 3, respectively; $F(2,44) = 43.7$, $p < .001$]. These results indicate that a significant familiarization with the task was already established after block 1 (420 trials), with no further difference between blocks 2 and 3, consistent with previous reports using the same task (Karni & Sagi, 1991; Schwartz et al., 2002; Stickgold et al., 2000). There was no main effect or interaction involving the visual field factor (training in upper vs. lower VF). Note that in all our analyses, data were collapsed across the two training sides (left or right, randomized across subjects), as there were no relevant differences between these stimuli (Fig. 1A) and no differences in task performance.

During EEG recording on the second day (post-training), behavioral results confirmed that the 500 ms SOA allowed us to obtain equal task difficulty across experimental conditions for both the letter identification (⩾98% correct across all blocks) and texture discrimination (⩾95%), in both the upper and lower VF groups. Non-parametric statistical analyses of performance on each task did not disclose any difference between groups (upper vs. lower VF, all $p > .10$; performance difference <1%) or between conditions (trained vs. untrained quadrant, all $p > .10$; performance difference <1.5%).

Critically, however, TDT thresholds measured on the testing day (24 h after training) clearly demonstrated location-specific perceptual learning (Karni & Sagi, 1991; Schwartz et al., 2002; Stickgold et al., 2000). These threshold values were submitted to an ANOVA with one within-subject factor (trained vs. untrained quadrant) and one between-subject factor (upper vs. lower VF group). This revealed a highly significant main effect of learning [$F(1,21) = 9.22$, $p = .006$; mean threshold = 98 ± 30 vs. 76 ± 31 ms for untrained vs. trained quadrants]. Although the interaction was not significant [$F(1,21) = 2.65$, $p = .12$], we performed planned comparisons to better characterize the learning effect in each group using paired t-tests. We found a significant effect of learning for upper VF subjects [$t(11) = 3.28$, $p = .007$; mean threshold = 78 ± 20 vs. 111 ± 32 ms for trained vs. untrained quadrants], whereas this effect was not significant in the lower VF [mean thresholds = 75 ms ± 38 vs. 85 ms ± 27 for trained vs. untrained quadrants, $t(11) = 1.00$, n.s.; see Fig. 2].

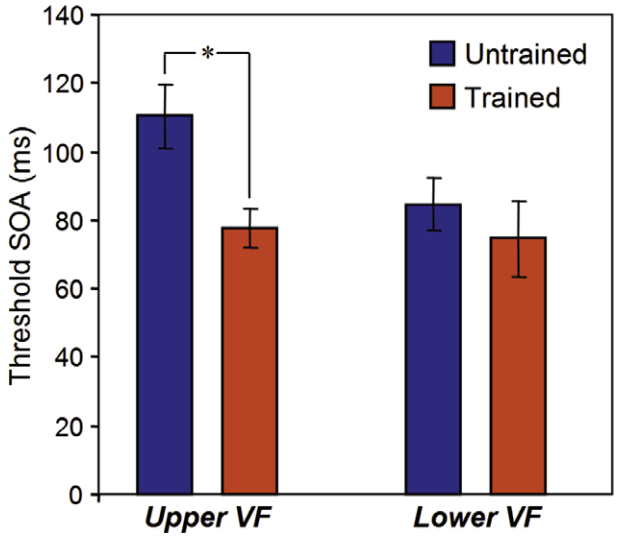

Fig. 2. Texture detection in trained and untrained quadrants on the testing day. Thresholds were computed for each individual as the SOA value for 80% correct texture detection; *$p < .05$.

Taken together, these behavioral data demonstrate a long-lasting benefit on TDT performance for the trained quadrant 24 h after intensive practice in upper VF, but no effect after practice in lower VF.

3.2. EEG data

In line with the behavioral results, perceptual learning produced robust changes in early cortical responses for subjects trained in the *upper VF*. First, GFP analysis revealed a significant reduction in the electric field strength evoked by targets in the trained versus untrained quadrant, arising from 44 to 102 ms post-onset [$t(11) = 2.35$, $p = .022$ (one-tailed); Fig. 3A]. Such GFP changes suggest robust effects on EEG activity, with a substantial extent across different electrodes over the scalp. We also submitted voltage differences between the trained and untrained conditions to an electrode-by-electrode paired *t*-test for each time-point during this period of significant GFP difference. This revealed that the training-induced changes were significant only for posterior electrodes over occipito-parietal sites, in keeping with the typical topographic distribution of C1. On the other hand, subjects trained in the *lower VF* showed no significant differences in GFP between the trained and untrained quadrants (Fig. 3B).

A typical C1 waveform with a large amplitude (Fig. 3) was reliably obtained during the same time-window for every participant, in both the upper and lower VF groups, consistent with a strong response of V1 to peripheral visual arrays of high-contrast line-elements (Clark et al., 1995). The polarity inversion (negative vs. positive activity over posterior midline electrodes) and slight peak-latency difference between the upper and lower VF (~85 ms vs. ~75 ms post-stimulus, respectively; $F(1,22) = 6.7$, $p = .017$) are also consistent with previous reports on C1 (Jeffreys & Axford, 1972; Lehmann & Skrandies, 1979). We tested for any learning-dependent changes in this component using repeated-measure ANOVAs on amplitude differences between conditions (targets at trained minus untrained locations), with electrode locations (Anterior-Central-Posterior and Left-Central-Right for electrodes CP1, CPz, CP2; P1, Pz, P2; PO3, POz, PO4) as within-subject factors and VF position (Upper-Lower) as between-subject factor. Results showed a significant interaction between learning and position in the upper versus lower VF [$F(1,22) = 7.8$, $p = .011$]. This was due to reduced C1 amplitude for trained targets in the upper VF (Fig. 3A), but no such effect for trained targets in the lower VF (Fig. 3B). Indeed, separate ANOVAs in each VF group confirmed a significant reduction of C1 amplitude following training in upper VF [$F(1,11) = 5.3$, $p = .042$], but indicated no reduction in lower VF subjects. In each group, peak latency differences between trained and untrained conditions were smaller than our 2 ms sampling period and therefore not followed up.

Taken together, these data indicate that similar visual targets in TDT displays could produce different cortical responses in the early C1 time-range when presented at a previously trained location relative to an untrained location (in upper VF), resulting in retinotopically selective changes in amplitude (but not in latency). We also tested for any topographic differences associated with these early cortical responses. Voltage maps covering the C1 time-window for each group were submitted to a standard microstate analysis (Pasqual-Marqui et al., 1995). This analysis did not reveal any significant differences in scalp topographies between training conditions, indicating that neural generators underlying the C1 component were the same in the trained and untrained conditions in both groups. Distributed source localization analyses showed that these generators were primarily located in early visual cortices, in accordance with the known properties of the C1 (Fig. 4; Clark et al., 1995; Foxe & Simpson, 2002).

Next, we examined whether learning could also modulate the subsequent VEPs that are typically affected by top-down attention, namely P1 and N1 (Heinze et al.,

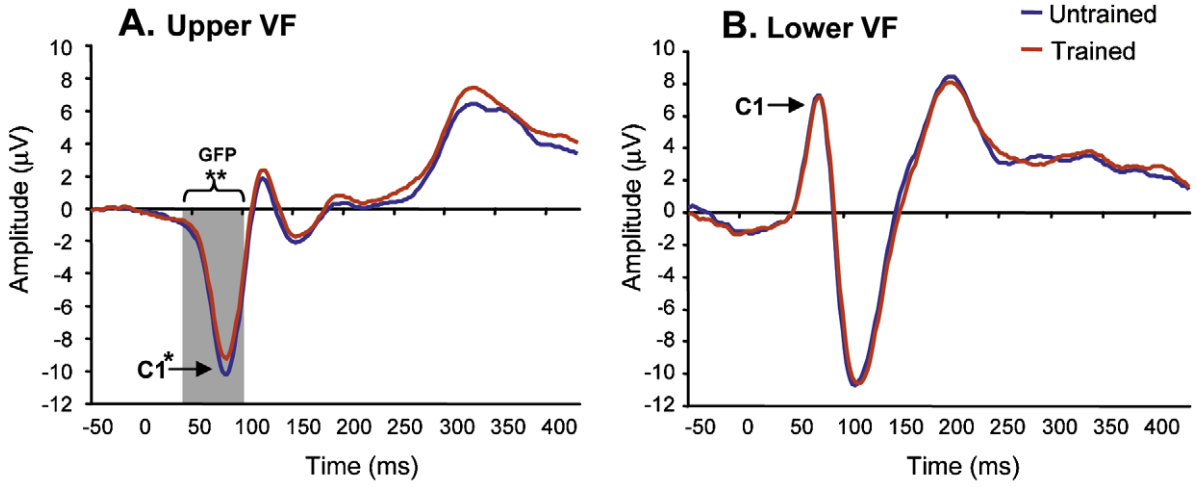

Fig. 3. Averaged C1 illustrated here at electrode Pz for trained and untrained quadrants. (A) Subjects trained in upper visual field, with time-window of learning-related GFP difference shown in light gray; (B) subjects trained in lower visual field; $^{*}p < .05$; $^{**}p < .01$.

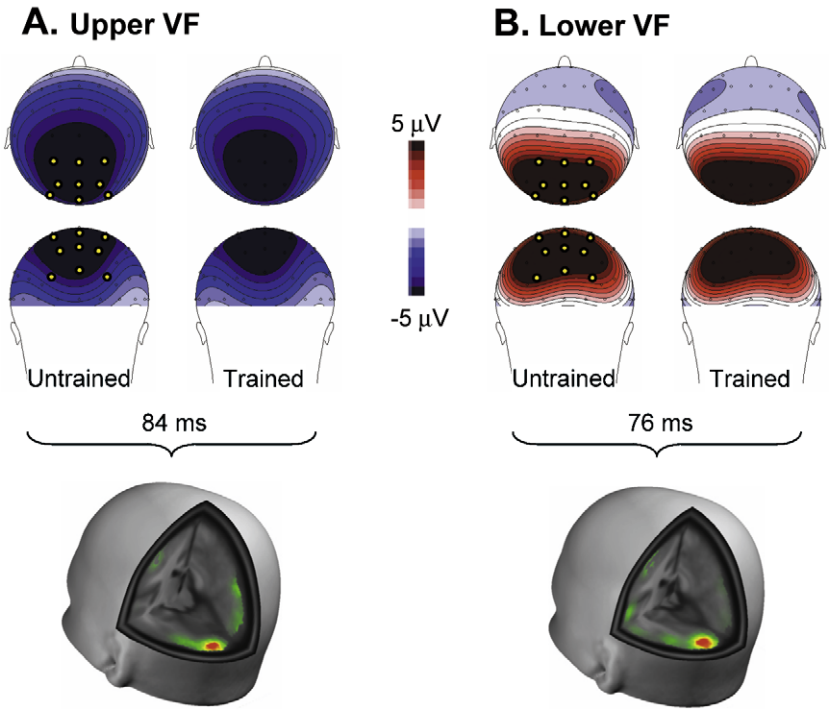

Fig. 4. Scalp current density maps at C1 peaks and retinotopic V1 sources for stimuli presented in (A) upper and (B) lower visual field. Positions of the 9 relevant electrodes used for C1 analyses are shown in yellow. Data for the distributed source localization are averaged across training conditions, because microstate analyses demonstrated equivalent topographies for trained and untrained conditions within each group (see text).

1994; Martinez et al., 1999). An ANOVA with the factors Training, Hemisphere, and Electrode (PO8/PO6/P8/P6 and symmetrically PO7/PO5/P7/P5) was performed on P1 peak amplitude (maximal ~130 ms post-onset) in upper VF subjects, but showed no significant effects of interest. In lower VF subjects, we did not observe a reliable P1 (presumably because it was generally cancelled out by the large positive C1 evoked in this condition); instead we observed a centrally distributed negative component (maximal at ~105 ms; Fig. 3B), with characteristics similar to a N90op (occipito-parietal; cf. Clark et al., 1995). As for P1 in upper VF, there was no significant effect of Training on the amplitude of this component (Pz, POz, Oz). No effect was found on latency measures for either P1 or N90op. Finally, training did not reliably modulate the amplitude of the N1 component (peak at ~160 ms) in any of the groups, and analyses of peak latencies for this component did not show any training-related effects either (cf. Fig. 3).

4. Discussion

By selectively training and testing visual quadrants at symmetrical retinal locations during TDT, and comparing targets at trained versus untrained positions, we were able to show for the first time that perceptual experience may result in a modulation of the retinotopic C1 component, associated with an early and sustained change in global field power from 44 to 102 ms post-stimulus onset. Critically, the behavioral improvement in TDT as well as the neural changes indexed by EEG activity were observed 24 h after training took place. Furthermore, both behavioral and EEG effects were found only in subjects who were trained in the upper visual field and not in those trained in the lower visual field.

Our findings reveal that perceptual learning may influence specific components in the sequence of neuronal events associated with the processing of trained visual configurations. The learning-related modulation of C1 contrasts with a lack of modulation of this early retinotopic component by other task-related factors, such as selective attention, as previously shown by numerous EEG studies (Clark et al., 1995; Di Russo et al., 2003; Fu, Greenwood, & Parasuraman, 2005; Martinez et al., 1999; Noesselt et al., 2002). Changes in C1 amplitude as a function of higher-level stimulus attributes have been reported during rapid presentation of emotional stimuli (Pourtois, Grandjean, Sander, & Vuilleumier, 2004) and following emotional conditioning (Stolarova, Keil, & Moratti, 2006). Previous work examining the effects of perceptual learning on early visual processing, on the other hand, did not specifically look for changes in the C1 component and is thus not directly comparable to our study due to differences in experimental setups. Skrandies and co-workers examined the effects of perceptual learning on ERP topography in Vernier acuity tasks (Ludwig & Skrandies, 2002; Shoji & Skrandies, 2006; Skrandies & Fahle, 1994; Skrandies, Jedynak, & Fahle, 2001). They observed topographic and latency effects of learning (starting from around 90 ms) when using stimuli presented either at central locations

(Skrandies & Fahle, 1994; Skrandies et al., 2001), or along the horizontal meridian (Ludwig & Skrandies, 2002), or simultaneously in all four quadrants (Shoji & Skrandies, 2006). No component matching the characteristics of the C1 is reported in any of theses studies. To our knowledge, long-lasting and retinotopically-specific effects of non-emotional stimuli on this earliest component of the visual evoked potential have not been demonstrated before. The use of large displays with high contrast elements eliciting a sizable C1 was necessary for detecting these subtle effects, as they are overlaid by large individual differences in the functional anatomy of early visual cortex (Dougherty et al., 2003). Our results therefore suggest that intrinsic plasticity in primary sensory cortices may underlie the consolidation of a newly acquired perceptual skill, and shape the initial volley of sensory inputs through the visual system (Foxe & Simpson, 2002).

A second important finding of our study is the spatial selectivity of these learning effects, with both behavioral improvement and neurophysiological changes arising only after training in the upper visual field. Taken together, our data provide new insights into the nature of learning-related changes in sensory responses of human V1, and constrain recent theoretical models of neural plasticity, as we discuss below in more detail.

4.1. Neural bases of perceptual learning

A plausible neural mechanism for perceptual learning in TDT involves strengthening of intrinsic connectivity between V1 neurons, in the absence of changes in basic receptive-field properties (Tsodyks & Gilbert, 2004). Top-down or reentrant influences operate on V1 to produce retinotopic increases in sensory response following the initial volley of visual inputs (Martinez et al., 1999; Noesselt et al., 2002). However, early reductions of GFP and C1 amplitude for trained stimuli (in upper VF), as observed in our study, suggest local changes within V1 after TDT learning, rather than later, reentrant influences. Importantly, any sustained top-down mechanisms would imply an interaction with local plasticity within V1 for the trained location (Li, Piech, & Gilbert, 2004), because the behavioral task and target-textures were identical for trained and untrained conditions, and because any training-related differences in attention orienting towards the target side were cancelled by using blocked presentations for each hemifield.

The observed significant *reduction* of early electrical activity for trained visual configurations provides new empirical support for recent computational models (Tsodyks & Gilbert, 2004) according to which learning biases intracortical inputs in favor of inhibitory activity to increase the discrimination of trained targets relative to background flankers (Herzog & Fahle, 1998; Tsodyks & Gilbert, 2004). Such interactions between excitatory and inhibitory processes in TDT learning may explain why discrimination of learned targets is impaired when background flankers are changed (Karni & Sagi, 1991).

These models may also account for the fact that trained stimuli produce an increase of BOLD signal in V1, as shown by previous fMRI studies of TDT (Schwartz et al., 2002; Walker et al., 2005) and other perceptual learning tasks (Furmanski et al., 2004; Sigman et al., 2005). Because BOLD signal is strongly modulated by the temporal structure rather than the total amount of synchronous neuronal discharges (Niessing et al., 2005), enhanced suppression of non-target background stimuli might increase BOLD signal, while reducing GFP and C1 amplitude at the scalp.

Critically, previous neuroimaging studies using fMRI could not unambiguously attribute learning-related V1 changes to early rather than later, reentrant stages of visual processing (Noesselt et al., 2002; Schwartz et al., 2002). In contrast, here we show neurophysiological changes implicating specific components associated with early sensory responses in striate cortex.

4.2. Visual field asymmetries in perceptual learning

Although we found clear behavioral and neurophysiological effects of learning for subjects trained in the upper visual field, we did not observe corresponding effects in the lower visual field. Asymmetries between upper and lower VF have been reported in many previous studies, including a latency shift of VEPs in favor of lower VF that corresponds well with our own results (Lehmann & Skrandies, 1979). Such differences have often been attributed to environmental constraints favoring the processing of complex textures in lower VF (Rubin, Nakayama, & Shapley, 1996; Skrandies, 1987). In contrast, we found no performance advantage prior to training and a lack of learning benefits in lower VF.

To our knowledge, no studies using the TDT have directly compared learning effects in the upper and lower VF. Moreover, some studies where subjects were only presented with lower VF stimuli have reported an initial deterioration of performance in TDT after training (Censor, Karni, & Sagi, 2006; Mednick, Arman, & Boynton, 2005). Thus, a reduction of performance due to intensive training sessions (Ofen, Moran, & Sagi, 2007) may occur more rapidly in lower VF and subsequently interfere with long-term consolidation processes (Censor et al., 2006). An alternative account of upper vs. lower VF asymmetries in TDT is suggested by Carrasco and co-workers (Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998) who demonstrated that higher spatial resolution close to the fovea may interfere with visual texture processing, and that such effects are stronger in lower VF due to its higher contrast sensitivity. Thus, higher spatial resolution in lower VF may interfere with effective learning in our task. However, more research is needed to fully elucidate the perceptual mechanisms underlying these asymmetries and their neural correlates.

5. Conclusions

Our results show that intrinsic plasticity in adult primary visual cortex may underlie the consolidation of a learned perceptual skill, leading to durable changes (>24 h) at early stages (<85 ms) of the visual cortical response to trained stimuli, presumably involving the very first cortical relay of inputs within V1. The observed asymmetry between upper and lower visual field may indicate differences in perceptual learning efficacy depending on retinotopic location and should be addressed more systematically in future research.

Acknowledgments

We thank C. Michel and two anonymous reviewers for helpful comments. This work was supported by grants from the Swiss National Science Foundation (#3100A0-102133; #632-65935; #51A240-104897), and by a grant from the Geneva Neuroscience Center.

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